FURTHER STUDIES ON THE TREMATODE GENUS HIMASTHLA WITH DESCRIPTIONS OF H. MCINTOSHI N. SP., H. PISCICOLA N. SP., AND STAGES IN THE LIFE-HISTORY OF H. COMPACTA N. SP.

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The genus *Himasthla* is a member of the Echinostomatidae, a family which comprises a large number of genera and species that live in the digestive tracts of birds and mammals. Dietz (1909) erected the genus with *H. rhigedana,* a new species from the curlews, *Numenius arquatus* and *Numenius arabicus,* as type. He (1910) characterized the family and the several genera. As members of *Himasthla* he included *H. militaris* (Rudolphi, 1803) from the European curlew, *Scolopax* (= *Numenius*) *arquata; H. leptosoma* (Creplin, 1829) from *Tringa alpina* (= *variabilis*); *H. elongata* (Mehlis, 1831) from species of gulls, *Larus; H. secunda* (Nicoll, 1906) from the black-headed gull, *Larus ridibundus* and the herring gull, *Larus argentatus;* and *H. alincia* Dietz, 1909, based on specimens from the semipalmated sandpiper, *Tringa pusillus* collected by Natterer in Brazil. The first of these species was taken on the Sinai peninsula, the last in South America, while the others were European. As important criteria for specific determination, Dietz listed the number of spines on the collar, the extent of the vitellaria, and the structural details of the copulatory organs.

Subsequently described species include *H. harrisoni* Johnston, 1917 from *Numenius cyanopus* in Australia; *H. incisa* Linton, 1928 from the white-winged scoter, *Oidemia deglandi,* at Woods Hole, Massachusetts; *H. muehlensi* Vogel, 1933 from a human patient in Hamburg, Germany; *H. ambigua* Palombi, 1934, based on encysted metacercariae from the gills of *Tapes decussatus* in the Mediterranean; *H. kusasigi* Yamaguti, 1939 from *Tringa ochlopus* and *H. megacotyle* Yamaguti, 1939 from *Erolia alpina sakhalina,* both species taken in Japan; *H. multilecithosa* Mendheim, 1940 from a captive great crowned pigeon, *Goura coronata;* and *H. tensa* Linton, 1940 reported from a codfish, *Gadus morrhua,* at Woods Hole, Massachusetts. Stunkard (1934, 1937, 1938) showed that *Cercaria quissetensis* Miller and Northup, 1926 is the larval stage of a species of *Himasthla,* for which the larval name was adopted. The asexual generations occur in *Nassarius obsoletus,* the cercariae penetrate and encyst in different species of mollusks, and the worms become sexually mature in the intestine of gulls. Prudhoe (1944) described, but did not name, a single specimen from the yellow-wattled lapwing, *Lobipluvia malabarica,* and assigned it provisionally to the genus *Himasthla.*

Metacercariae from the foot of *Scrobicularia tenuis* were identified as *Cercaria leptosoma* by Villot (1878), who traced their development to maturity in the

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alimentary tract of the "allouette de mer à collier." *Tringa variabilis*. The number of collar-spines was not recorded, but the figure of the adult is very similar to that of *H. leptosoma* as given by Dietz. Cuénot (1892) reported metacercariae of *H. leptosoma* encysted in the circumoral tentacles of *Synapta inhaerens* and in the foot of *S. tenuis*, but since he found 31 or 32 collar-spines, it is obvious that he was dealing with some species other than *H. leptosoma*. Palombi (1925) identified metacercariae from *Mytilus galloprovincialis* as larvae of *Echinostomum secundum* (= *H. secunda*) Nicoll, 1906. Skrjabin (1956) included figures of the larval stages of *H. militaris* after the work of Zelikman, but there was no account of the life-cycle or reference to other published report.

There has been much difference of opinion concerning specific distinctions and the number of valid species in *Himasthla*. Stunkard (1939) reviewed the history of the genus and discussed the problem of specific determination. Linton (1928) had described specimens from four species of gulls (*Larus*) and others from the white-winged scoter, *Oidemia deglandi*, and from the black-crowned night heron, *Nycticorax nycticorax*. The worms from *O. deglandi* were described as a new species, *H. incisa*, while all the others were referred to *H. elongata*, despite differences in number of collar-spines and other morphological features. Some of the worms had 29, others 31 collar-spines, and it was clear that two distinct species were represented. Those with 31 spines were identified by Stunkard (1938) as *H. quissetensis*, whereas those with 29 spines were intermediate in size and morphology or overlapped the figures given by Dietz (1910) as characteristic for *H. elongata* and *H. militaris*. Stunkard (1938) stated, p. 190, "In my opinion the worms might with equal justification be referred to either of the two species. On the other hand, they may belong to neither." Sprehn (1932) listed *H. militaris* and *H. secunda* as synonyms of *H. leptosoma* and Palombi (1934) admitted the probable identity of *H. leptosoma* and *H. secunda*. Stunkard noted similarity between *H. alincia* and *H. quissetensis* and conceded their possible identity. Dawes (1946) regarded *H. leptosoma* and *H. elongata* as valid species, but listed *H. militaris* and *H. secunda* as synonyms of *H. leptosoma*.

In correspondence with Dr. Vogel, Dr. Mendheim accepted the opinion of Sprehn (1932) and in addition predicated the identity of *H. elongata* and *H. leptosoma*. With this proposal, all the specimens of *Himasthla* with 29 collar-spines were included in a single species, *H. elongata*. However, if the idea were correct, the name of the species must be *H. militaris* (Rudolphi, 1803), which has priority over *H. elongata* (Mehlis, 1831). In addition, Dr. Mendheim suggested the identity of *H. muehlensi* and *H. elongata*. The specimens of *H. muehlensi* had been recovered from the stool of a patient following a purgative after his arrival at the hospital of the Institut für Schiffs- und Tropenkrankheiten in Hamburg, Germany. The patient was a South American who had stopped at New York on his way to Germany and in sea-food restaurants had eaten many "clams," juvenile *Venus* (*Mercenaria*) *mercenaria* which are served raw on the half-shell under the designation "cherry stones." In his description of the specimens, Vogel (1933) noted that members of *Himasthla* are typically parasites of birds and that the human infection was a recent and probably an accidental one. In a monographic study of the Echinostomidae, Mendheim (1940) described *Himasthla multilecithosa* n. sp., from *Goura coronata*, a native of the Papuan and Solomon Islands. Mendheim reported

that the time and place of the infection were unknown, that the normal food of these birds is fruit, and since the infective larvae of *Himasthla* occur in marine mollusks, the infection must have been accidental or incidental. After redescriptions of *H. elongata* and *H. muehlensi* he wrote, p. 578, "Auf Grund einiger Befunde müssen *Himasthla leptosoma, Himasthla elongata* und *Himasthla muehlensi* zu einer Art vereinigt werden." But his account of *H. elongata* was obviously based on material of more than one species since he reported the number of collar-spines as 29–31. His report on the specimens of *H. muehlensi,* loaned by Dr. Vogel, adds nothing of significance to the original description. He noted that egg production had just begun and that the first eggs were smaller than those formed later, from which he concluded, p. 511, "Die Eimasse können also nicht als brauchbares Artkriterium gelten." The observation is not new (q.v., Beaver, 1937, p. 26) and the conclusion is equivocal.

The writer had the opportunity in Hamburg to study the specimens of *H. muehlensi,* several specimens of *H. leptosoma* from *Tringa alpina* in the collection of Dr. Vogel, and four specimens sent by Dr. Mendheim that were identified as *H. elongata.* In a report, Stunkard (1939) stated that the specimens of *H. muehlensi* have 31 collar-spines and while there is a possibility that they may be identical with *H. quissetensis,* they certainly are distinct from *H. elongata* which has 29 spines. Furthermore, although *H. elongata* and *H. leptosoma* both have 29 collar-spines, morphological differences, first listed by Dietz and manifested by specimens from the collections of Vogel and Mendheim, clearly differentiate the two species. Specimens of *H. leptosoma* are smaller, the structure is more delicate, the suckers, collar-spines and eggs are smaller, the vitellaria do not extend as far anteriad, and the gonads are larger. Mendheim (1943) reaffirmed the identity of *H. elongata, H. leptosoma* and *H. muehlensi,* which he derived from average measurements of 15 specimens which, according to the text, included the four worms identified by Stunkard as *H. elongata.* Since the author admittedly was unable to distinguish between *H. elongata* and *H. leptosoma,* and since it is apparent from his figures that the 15 specimens included representatives of both species, the average measurements are meaningless. In a key for determination of species, Mendheim (1943, p. 235) distinguished *H. incisa* on the basis of 27 collar-spines. In the original description Linton (1928) wrote, p. 12, "The exact number of oral spines could not be made out in the balsam mount. There are at least 27. There is a single row, except at the lateral angles." After examination of the type specimen, Stunkard (1938) reported that the worm has 31 spines. Re-examination of the specimen confirms that number; the spines are relatively stout and those in the single row measure 0.065 to 0.070 mm. in length. The slide bearing the single type specimen has a label written by Professor Linton noting that the worm was collected by Vinal Edwards, June 2, 1914, at Woods Hole, Massachusetts.

Linton (1940) described *H. tensa* as a parasite of *Gadus morrhua;* there are three specimens on the slide deposited in the U. S. National Museum and the notation, in Linton's handwriting, states that the worms were collected by Vinal Edwards, 1915. Mendheim apparently accepted the fish as a normal host. He stated, (1943, p. 235) "Besonders bemerkungswert ist *H. tensa* aus *Gadus morrhua.* Es ist dies seit dem von Diesing beschriebenen *Echinostoma annulatum* Diesing 1850 die einzige Echinostomiden-Art aus Fischen. Körperform, Lage des Bauch-

PLATE I

FIGURE 1. *Himasthla compacta*, type specimen; length 4.00 mm.

FIGURE 2. *Himasthla compacta*, cotype specimen; length 3.10 mm.

FIGURE 3. *Himasthla elongata*, juvenile specimen without eggs, from *Larus delawarensis*, taken 24 January 1914 at Woods Hole, Mass., by Vinal Edwards. Linton material now in U. S. National Museum Helminthological Collection, No. 7922; length 6.00 mm.

FIGURE 4. *Himasthla elongata*, from *Larus argentatus*, taken 18 December 1921 at Woods Hole, Mass., by R. A. Goffin. Linton material now in U. S. National Museum Helminthological Collection, No. 7921; specimen 8.75 mm. long.

FIGURE 5. *Himasthla elongata*, on same slide as Figure 4, same data; specimen 6.75 mm. long.

FIGURE 6. *Himasthla elongata prov.*, from night heron, *Nycticorax nycticorax*, taken 11 September 1914 at Woods Hole, Mass., by Vinal Edwards. Linton material now in U. S. National Museum, No. 7924; specimen 6.00 mm. long.

PLATE II

FIGURE 7. *Himasthla tensa* Linton, 1940. Type and cotype specimens from *Gadus morrhua*, taken 22 January 1915 at Woods Hole, Mass., by Vinal Edwards. Linton material now in the U. S. National Museum, No. 8214; type specimen at bottom of photograph; length, 5.32 mm.

saugnapfes und Pseudosegmentierung lassen es vor allem seit Linton's Fund als durchaus wahrscheinlich erscheinen, dass Diesing eine *Himasthla*-Art vorgelegen hat." *Distomum annulatum* was described by Diesing (1850) from the intestine of the electric eel, *Gymnotus electricus*. The specimens had been collected by Natterer in Brazil, the 3rd of September, 1827. In his description and figures, Diesing (1855) gave the length as 6 lines and the maximum width as ½ line, which would be slightly more than 12 by 1 mm. Cobbold (1860) transferred the species to *Echinostoma* and Dietz (1910) listed it under *Species inquirendae*. Mendheim noted features in which it conforms to the diagnosis of *Himasthla*. The specific name, *annulatum*, is significant since this feature is a prominent characteristic of the genus. Examination of the figures of Diesing (1855) and comparison

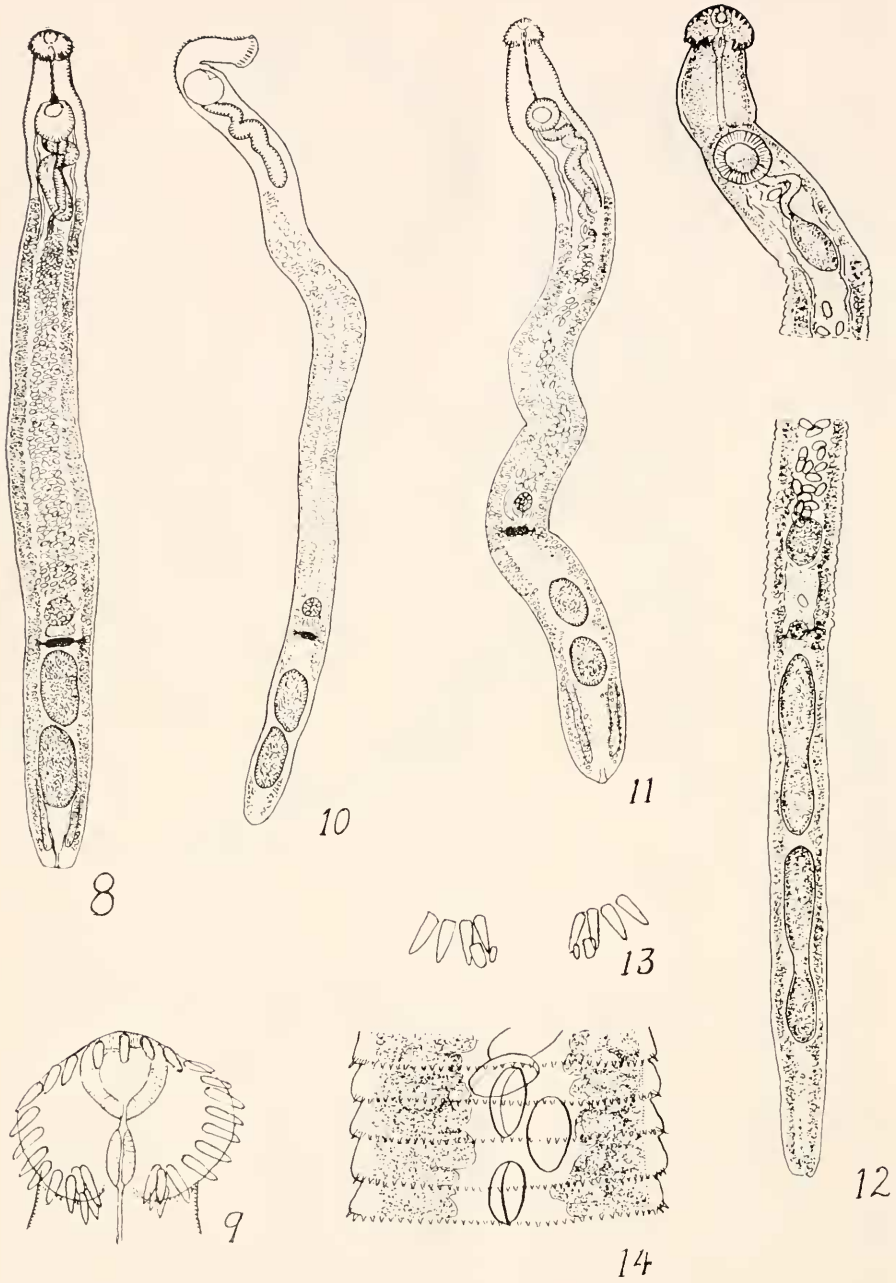


PLATE III

FIGURE 8. *Himasthla elongata*, drawing of specimen shown in Figure 5.
FIGURE 9. Collar and spines of specimen shown in Figure 8.
FIGURE 10. *Himasthla elongata*, drawing of specimen shown in Figure 3.

of his Figure 21, Plate III, showing five annuli, with Figure 14 of the present work, show that the worms described as *D. annulatum* agree far better with the generic concept of *Himasthla* than with that of *Echinostoma*. Accordingly they are transferred to that genus as *Himasthla annulata* (Diesing, 1850). Although *H. annulata* and *H. tensa* were described from fishes, each species has been found only once and there are strong reasons for regarding both of them as parasites of birds which were found incidentally in the intestine of the electric eel in Brazil and the codfish of New England, respectively.

Material and Methods

This report presents results from one section of the investigation conducted by the U. S. Bureau of Commercial Fisheries to discover causes for the decline in number of soft-shelled clams, *Mya arenaria*, along the coast of New England. To Walter R. Welch, Chief, Clam Investigations, and his staff in Boothbay Harbor, Maine, grateful appreciation is expressed for avian and molluscan specimens provided for the study. Other material was provided by the Marine Biological Laboratory, Woods Hole, Massachusetts, where the experimental work was done. Examination of clams from the region of Boothbay Harbor disclosed echinostome metacercariae encysted in the palps and gills. These larvae were fed over periods of one to seven weeks to laboratory-reared eider ducks (*Somateria mollissima*), herring gulls (*Larus argentatus*), terns (*Sterna hirundo*), white mice and golden hamsters. The worms excysted in eider ducks but did not persist more than about ten days. Adult worms were recovered from only one species, *L. argentatus*. Further study has shown that three species, all members of the genus *Himasthla*, are concerned. One of these species, *H. quissetensis*, was described by Stunkard who (1938) found the asexual generations in the mud-snail, *Nassarius obsoletus;* the life-history of another, described as *H. compacta* n. sp., is reported in the present paper; while the third species is identified as *H. elongata* (Mehlis, 1831). All three species have been recovered from the intestine of laboratory-reared gulls, *L. argentatus*, fed palps and gills of *M. arenaria* collected in the Boothbay Harbor area. To preclude accidental and complicating infections, the birds were fed commercial, canned cat-food, made from fishes and supplemented with vitamins. The examination of shore-birds in the Boothbay Harbor area disclosed a fourth species, identified as *H. alincia*, in the intestine of *Ereunetes* (*Tringa*) *pusilla*. This is the host from which the species was originally described by Dietz (1909).

To supplement the study of these worms, all specimens of *Himasthla* in the Helminthological Collection of the U. S. National Museum have been received on loan through the kindness of Dr. Allen McIntosh and the favor is here gratefully acknowledged. The collection contains several specimens from *Larus argentatus*

Figure 11. *Himasthla elongata*, drawing of specimen shown in Figure 6.

Figure 12. *Himasthla elongata*, a greatly extended specimen from the intestine of *Larus argentatus*, experimental infection; the bird had been fed metacercariae encysted in the gills and palps of *M. arenaria*. In the drawing, a section 6 mm. long, containing 110 annuli, is omitted from the middle of the body; specimen 12.5 mm. long.

Figure 13. Spines at the ventro-lateral corners of the collar; note the very small median spines.

Figure 14. Five annuli from the central portion of the specimen shown in Figure 12.

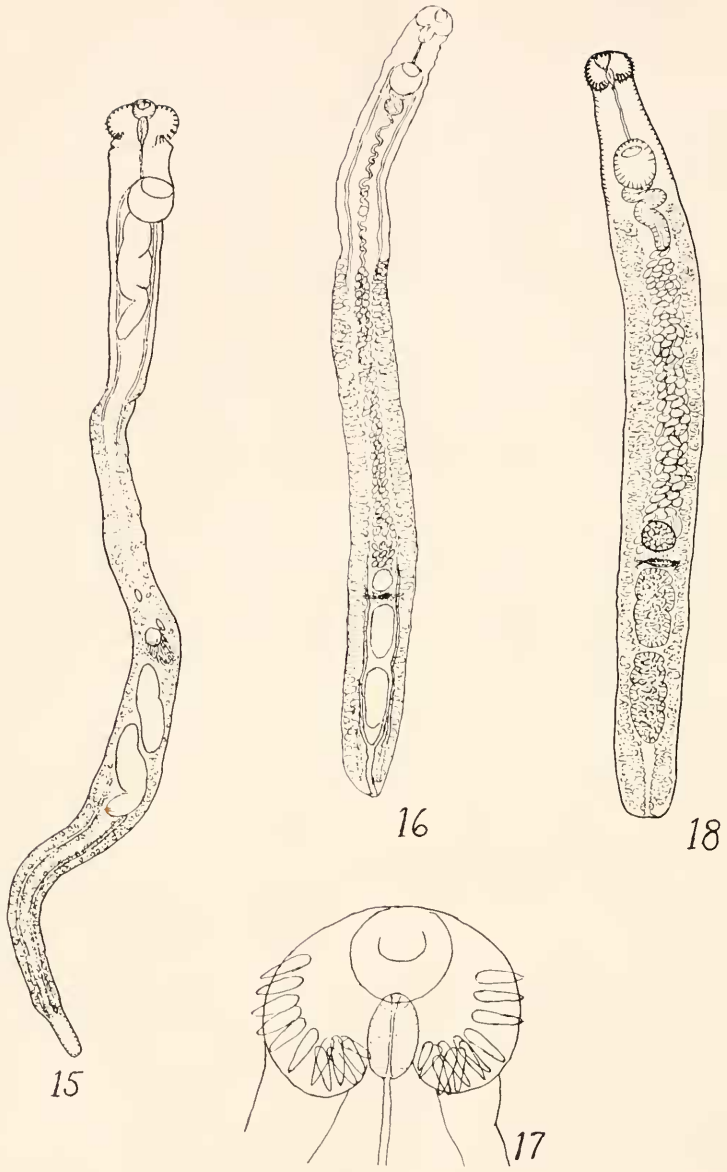
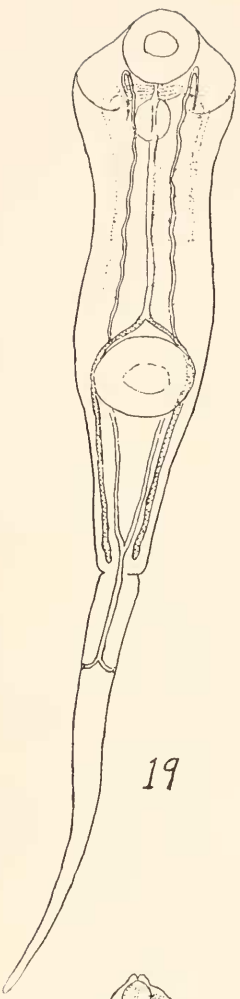


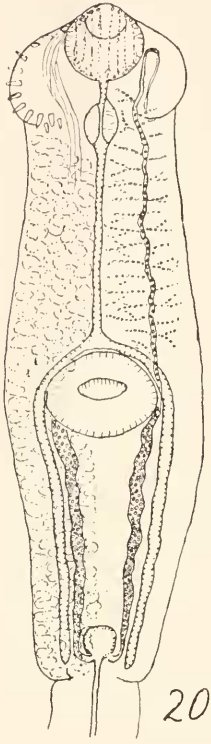
PLATE IV

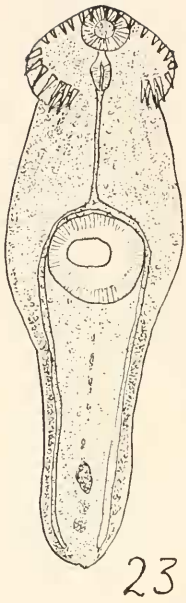
FIGURE 15. *Himasthla piscicola*, type specimen, length 9.80 mm.
FIGURE 16. *Himasthla mcintoshi*, type specimen, length 8.00 mm.
FIGURE 17. Spines at the ventro-lateral corners of the collar of worm shown in Figure 16.
FIGURE 18. *Himasthla compacta*, drawing of specimen shown in Figure 1.

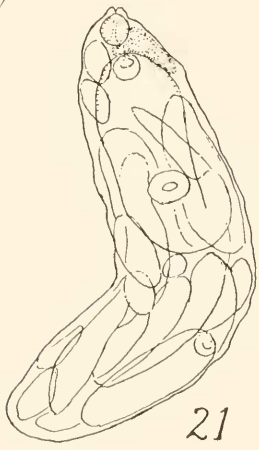
and one from *Nycticorax nycticorax* which had been identified by Linton as *H. elongata*. It contained, also, the type material of *H. incisa* Linton, 1928 and *H. tensa* Linton, 1940. Examination of the specimens of *H. tensa* discloses that the number of collar-spines is 29, not "about 32" as reported by Linton (1940). In the three specimens (Fig. 7), the vitelline follicles terminate a short distance posterior to the caudal end of the cirrus-sac. In the specimens of *H. elongata* shown in Figures 4 and 5, the vitellaria extend anteriad slightly past the caudal end of the cirrus-sac but in other individuals, especially younger ones, the vitellaria do not extend to the level of the cirrus-sac. No constant differences were found between these worms and, accordingly, the name *H. tensa* is suppressed as a synonym of *H. elongata*. The Museum Collection also contains four slides bearing the number 54,721, with seven specimens from the "long-billed curlew," *Numenius americanus americanus*, collected by J. Bushman at Orr's Ranch, Tooele Co., Utah, April 21, 1954. These worms have 35 collar-spines and are described as a new species, *Himasthla mcintoshi*. Subsequently, Dr. George R. La Rue of the Research Center, U. S. Department of Agriculture, Beltsville, Maryland, sent two specimens taken from the digestive tract of a South American fish, *Arapaima gigas*, that died in the Toledo, Ohio, zoo and that had been referred to him for identification. Grateful acknowledgment is made also to Dr. La Rue for the privilege of examining and describing these worms.

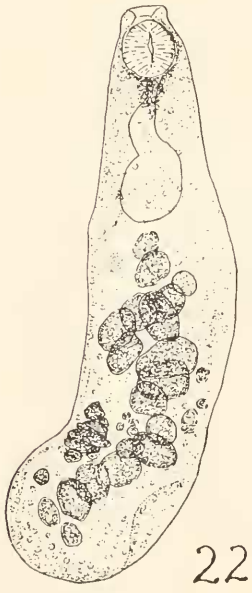
To locate the asexual generations of the metacercariae which occur in the gills and palps of *M. arenaria*, a survey of the mollusks in the Boothbay Harbor area was begun. As noted above, *N. obsoletus* had been identified as the first intermediate host of *H. quissetensis*. The first intermediate hosts of *H. elongata* and *H. alincia* are yet unknown, but there is strong and almost conclusive evidence that an echinostome cercaria from *Hydrobia minuta* is the larval stage of one of the metacercariae in *M. arenaria* and that this metacercaria develops in *L. argentatus* to adults described in this paper as *Himasthla compacta* n. sp. *Hydrobia minuta* harbors at least six different species of cercariae. Examination of 5000 snails, isolated 100 per dish, yielded three specimens shedding an echinostome cercaria and examination of 5000 snails in another series, in which an individual count was kept as the snails were crushed and examined under the microscope, disclosed six infections by this echinostome cercaria. It has 29 collar-spines and is the only echinostome cercaria, other than that of *H. quissetensis* which has 31 spines, found so far in the region. Very small specimens of *M. arenaria* collected in the Woods Hole, Massachusetts, area were added to the dishes containing the cercariae from *H. minuta* and metacercariae, presumably of experimental infection, were recovered from them. Owing to the low incidence of infection and the small size of the snails, and the resulting scarcity of cercariae, it has not been possible to produce massive infections which are easily obtained with the abundant cercariae of *H. quissetensis*. When using clams collected in the field, there is the possibility that they may be carrying metacercariae of natural infection, but examination of 200 specimens from the area where those used in the experiment were taken, revealed no infection. Since laboratory-reared clams were not available, very small clams from the Woods Hole area were employed. These clams, exposed to the cercariae, were fed subsequently to a young, laboratory-reared gull, *L. argentatus*. The bird began to pass trematode eggs some four weeks after the first feeding and later, on examination, it contained 26 small











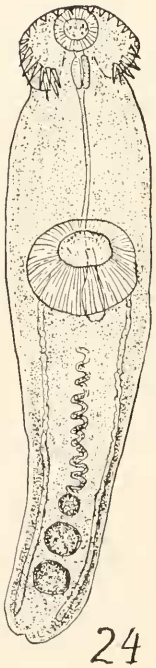


PLATE V.

echinostomes, identified as *H. compacta* n. sp. This species has 29 collar-spines and identification of the larval stages is not easy. The sizes of the cercariae and of their metacercariae are not significantly different from those of *H. quissetensis* and do not provide certain criteria for specific determination of the larvae. The adults are distinguished easily. Consequently, it appears that one of the best means of positive identification is to expose small clams to the cercariae and then feed the metacercariae to previously unexposed birds.

Additional data on the life-cycle are provided by results of attempts to infect the snail host. Eggs of *H. compacta,* taken from worms that had developed in a laboratory-reared gull, were incubated in sea-water at room temperature. At the end of four weeks they contained fully formed miracidia and were added to a finger-bowl containing 20 juvenile *H. minuta.* Four weeks later the number of living snails was reduced to 13. Snails that died were not examined, since the tissues decomposed quickly and trematode larvae would probably not be recognizable. One snail, dissected four weeks after exposure, contained three small rediae (Fig. 22) but whether they were mother or daughter rediae was not determined. No cercariae were obtained and the experiment was disappointing; however, it illustrates the difficulties inherent in this type of research. The number of eggs was limited, development seemed to proceed at variable and inconstant rates, and actual hatching was not observed. Since individual exposure of a snail to one or more miracidia could not be made, the mass exposure method was undertaken to determine whether or not certain of the miracidia on emergence could find and infect snails. With such "shotgun" technique, it is impossible to know how many, if any, miracidia penetrated a particular snail and it is possible that the death of certain snails was caused by superinfection. The one experimental infection, however, supplements other data and strongly supports the postulated life-cycle.

Descriptions

Himasthla elongata (Mehlis, 1831)

Linton (1928) described trematodes from *Larus argentatus* at Woods Hole, Massachusetts, which he identified as *Himasthla elongata.* Stunkard (1938) pointed out that the material of Linton comprised two distinct species, one of which was identified as *Himasthla quissetensis,* whose cercarial stage had been described

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PLATE V

Figure 19. *Himasthla compacta,* young cercaria from *Hydrobia minuta,* natural infection, specimen fixed and stained; body 0.50 mm. long; tail 0.37 mm. long; to show digestive, nervous and excretory structures.

Figure 20. *Himasthla compacta,* normally emerged cercaria, sketch of living specimen to show glands and excretory ducts.

Figure 21. *Himasthla compacta,* redia, natural infection, fixed and stained; specimen 1.12 mm. long.

Figure 22. *Himasthla compacta,* redia, experimental infection, fixed and stained; specimen 0.47 mm. long.

Figure 23. *Himasthla compacta,* young specimen from gull, fixed and stained; 0.46 mm. long.

Figure 24. *Himasthla compacta,* young specimen from gull, fixed and stained; 0.76 mm. long.

and named by Miller and Northup (1926). The members of the other species were not identified although Stunkard noted that measurements of 12 representative specimens are intermediate between or overlap the figures given by Dietz (1910) as characteristic for *H. elongata* and *H. militaris*.

Certain of the adult worms recovered from the intestine of *L. argentatus* after feeding metacercariae encysted in the tissues of *M. arenaria* from Maine are identified as *H. elongata*. These worms unquestionably are specifically identical with those identified as *H. elongata* by Linton (1928). In most of the specimens the collar-spines are slightly larger and the testes considerably larger than the figures given by Dietz (1910) for *H. elongata* but there is considerable variation, and the location of the testes and ovary near the posterior end of the body clearly differentiates them from *H. militaris*. One specimen, killed in a very extended condition (Figs. 12, 13, 14), exhibits the pseudosegmentation characteristic of the postacetabular region of the body and the annular arrangement of the flattened, scale-like spines. In this specimen, the two median members of the corner-spines (Fig. 13) on the collar are very small, recalling the condition shown in Figure B[1] of Dietz. The worm measures 12.5 mm. in length and 0.45 mm. in greatest width. In Figure 12, 6 mm. and 110 annulations are omitted from the middle of the body. Five of the annuli are portrayed in Figure 14. Another, younger specimen, with a few eggs in the uterus gave the following measurements: length, 4.4 mm.; width, 0.5 mm.; width at collar, 0.3 mm.; spines, 0.058 mm. long; acetabulum, 0.31 mm. long and 0.26 mm. wide; oral sucker, diameter 0.11 mm.; pharynx, 0.098 mm. long and 0.056 mm. wide; vitellaria do not extend forward to the level of the cirrus-sac; ovary 0.156 mm. wide and 0.125 mm. long; anterior testis, 0.25 mm. long and 0.155 mm. wide; posterior testis, 0.28 mm. long and 0.15 mm. wide; eggs 0.090 to 0.100 mm. long and 0.060 to 0.068 mm. wide. Gravid worms vary in size from these measurements to older individuals that are twice as large with correspondingly larger organs, but the structural pattern of the species is always evident.

The single specimen from the night heron, *N. nycticorax*, shown in Figures 6 and 11, has 29 collar-spines but manifests certain differences from the worms found in *L. argentatus*. It is only slightly smaller than the worm shown in Figure 5; however, the collar-spines and suckers are smaller, the vitellaria do not extend as far anteriad, and the gonads are smaller and slightly farther forward. In this specimen the spines are 0.050 mm. long; the oral sucker measures 0.114 by 0.107 mm.; the acetabulum is 0.325 mm. long and 0.290 mm. wide; the ovary is spherical, 0.143 mm. in diameter; the anterior testis is 0.40 mm. long and 0.23 mm. wide; the posterior testis is 0.42 mm. long and 0.25 mm. wide; the eggs average 0.097 by 0.062 mm. The measurements are almost identical with those given by Nicoll for *Himasthla secunda*, and the small size of the gonads agrees well with the description of *H. elongata* as given by Dietz. The similarity suggests possible identity of *H. secunda* and *H. elongata*. Since the material at hand consists of a single specimen, it is referred for the present to *H. elongata*. When the life-history of that species is known and cercariae are available for experimental infections, it will be possible to determine definitely whether the present worm belongs in *H. elongata* or is a member of some other species.

The specimen from *Larus delawarensis* (Fig. 3) is referred to *H. elongata*, but it is juvenile and possibly members of that species do not attain sexual maturity in *L. delawarensis*.

Himasthla compacta n. sp.

Adult

Material of this species consists of worms recovered from laboratory-reared *L. argentatus* fed *M. arenaria* collected near Boothbay Harbor, Maine, and others from another laboratory-reared *L. argentatus*, five weeks after the beginning of an experiment in which the bird was fed metacercariae encysted in small *M. arenaria*. These clams had been exposed to echinostome cercariae from *H. minuta* collected in Sagadahoc Bay, near Boothbay Harbor, Maine, and the metacercariae were presumed to be encysted stages of the same cercariae. Most of the worms were sexually mature but several were juveniles. The bird had been fed five weeks, two weeks and one week before it was killed and the small worms shown in Figures 23 and 24 are probably from the last two feedings. A specimen 2.130 mm. long and 0.275 mm. wide does not have eggs in the uterus, although there are spermatozoa in the testes.

Gravid specimens, fixed and stained, measure 3.00 to 4.30 mm. in length and 0.35 to 0.44 mm. in width. For such a small species of *Himasthla*, the organs are large and compactly disposed. The sides of the body are almost parallel; the acetabulum protrudes; in the preacetabular region the lateral edges are often turned ventrad and mediad, forming a ventral depression. The anterior end has a reniform collar, open ventrally, which bears 29 spines, 25 arranged in a linear row and two smaller corner-spines on each side behind the terminal ones of the row. The lineal spines are 0.054 to 0.062 mm. in length and 0.012 to 0.014 mm. wide; the smaller corner ones are 0.026 to 0.032 mm. long and 0.009 mm. wide. In mature specimens the acetabulum is about one-seventh of the body length from the anterior end whereas in juvenile worms it is relatively farther back and in young worms it is near the middle of the body. The shift in relative position of the acetabulum results from development of the reproductive organs in the postacetabular portion of the body. The acetabulum is usually longer than broad, oriented with the opening at the antero-ventral face, just behind the common genital pore. The sucker measures 0.20 to 0.26 mm. in length and 0.18 to 0.22 mm. in width. The cuticula in the preacetabular area bears scale-like spines arranged in an imbricate pattern, while behind the sucker the spines are smaller and are arranged in the annular fashion characteristic of the genus.

The mouth is subterminal; the oral sucker measures 0.075 to 0.090 mm. in diameter. There is a short prepharynx; the pharynx is oval to pyriform, usually wider posteriorly, it measures 0.060 to 0.075 mm. in length and 0.040 to 0.050 mm. in width. The esophagus extends almost to the acetabulum and the ceca end blindly near the posterior end of the body.

The testes are almost contiguous, one behind the other, in the caudal one-third of the body. They are oval, with notched but not lobed surfaces. The posterior testis is usually somewhat larger than the anterior one. The anterior testis is 0.36 to 0.49 mm. in length and 0.18 to 0.21 mm. in width; the posterior testis is 0.40 to 0.58 mm. in length and 0.18 to 0.21 mm. in width. From each testis a sperm duct passes forward and the two unite just before reaching the cirrus-sac. The common duct, on entering the sac, expands into a coiled seminal vesicle, which fills the posterior one-half or more of the cirrus-sac. The vesicle is followed by a shorter prostatic portion of the duct and then by a protrusible cirrus armed with very small

spines. The cirrus-sac extends behind the acetabulum more than the diameter of that sucker and terminates between the anterior ends of the vitelline glands.

The ovary is spherical to oval, usually broader than long, situated from two-sevenths to three-eighths of the body length from the posterior end. It is about its diameter in front of the anterior testis. It measures 0.06 to 0.13 mm. in length and 0.08 to 0.16 mm. in width. The oviduct arises at the posterior face and passes backward where it enters the ootype region. It expands somewhat and gives off Laurer's canal, which passes to the dorsal surface of the body, after which it receives the common vitelline duct. This portion is partially enclosed in the cells of Mehlis' gland, which surrounds the ootype. The initial portion of the uterus is filled with masses of spermatozoa. The uterus coils about and passes forward to the level of the caudal end of the cirrus-sac where it joins the metraterm. Both metraterm and cirrus-sac pass forward above the acetabulum to open into a shallow genital sinus, and the genital pore is on the median ventral surface, immediately anterior to the acetabulum. The vitelline follicles are lateral to and partially overlap the digestive ceca; they extend from the caudal end of the body to a level about the length of the acetabulum behind that sucker. They are not interrupted at the levels of the testes. Longitudinal ducts connect the follicles and transverse ducts pass mediad at the level of the ootype, where they unite to form a vitelline receptacle from which a common duct leads to the initial portion of the ootype. The eggs are large, oval, thin-shelled, collapsed in the preserved specimens, 0.085 to 0.090 mm. in length and 0.050 to 0.058 mm. in width. Each egg contains an ovum and several vitelline cells. The ovum is situated toward the opercular end of the egg. Cleavage begins in the uterus, but development there does not go much beyond the four-cell stage.

Himasthla compacta differs from all other species of the genus in its smaller size, its compact structure and relatively larger gonads. The ovary is situated about one-third of the body length from the posterior end and the testes extend through most of the postovarian distance, a condition not found in any other species. Since *H. compacta* has not been reported previously from *L. argentatus*, some other avian species may be its normal host.

The type specimen (Figs. 1, 18) is deposited in the U. S. National Museum Helminthological Collection under the number 39,444.

Redia

In structure and behavior, the rediae are very similar to those of *H. quissetensis* as described by Stunkard (1938). Figure 21 is a drawing of a large, gravid redia of natural infection. It is 1.12 mm. long and 0.28 mm. wide; the pharynx is 0.028 mm. in diameter. Figure 22 shows a young redia recovered from one of the small specimens of *H. minuta* which had been exposed for four weeks to embryonated eggs of *H. compacta* taken from worms that had developed in the intestine of a laboratory-reared specimen of *L. argentatus*. Whether this is a first or second generation redia could not be determined, since the germ balls in it could be embryos of either rediae or cercariae. At this stage they are quite indistinguishable. The specimen measures, fixed, stained and mounted, 0.47 mm. long, 0.12 mm. wide, and the pharynx is 0.027 mm. in diameter. The young rediae have collars which become visible as the larvae move; they progress in a lumbricid manner, with temporary protrusions of foot-like projections to anchor one region while advancing another. In young rediae

the gut is conspicuous, filled with yellowish-green material, obviously the residue from digestion of snail tissue. The intestine does not increase in size and becomes proportionately smaller as the cavity of the redia becomes filled with larvae of the next generation. With increase in size and accumulation of growing progeny, the rediae become less and less active. Meanwhile, with advancing maturity, the cercariae become more vigorous in their movements until they emerge through the birth-pore, situated near the pharynx.

Cercaria

The incidence of infection of *H. minuta* is low, about one in five hundred, and cercariae emerged from less than one-half of the infected snails. The snails are small and few cercariae are produced. They leave the rediae and complete development in the haemocoele of the snail. In a crushed snail with mature infection, usually there are two to four or five cercariae free in the sinuses and others still in rediae. Some of those in the rediae swim actively when released, but the small number of cercariae restricts experimental procedure. In swimming, the body is contracted until it is almost spherical while the tail is extended and lashes vigorously.

The body in living cercariae measures 0.30 to 0.60 mm. in length and 0.08 to 0.19 mm. in width; it is elongate oval in outline although the shape varies with the degree of elongation and retraction. The collar gives the anterior end a characteristic form and when the larva is fully extended, this may be the widest part of the body. The tail is shorter than the body and capable of great extension and retraction by contraction of the circular or longitudinal muscles which form its wall. In naturally emerged cercariae the oral sucker measures 0.057 to 0.065 mm. in diameter; the ventral sucker 0.072 to 0.086 mm.; and the pharynx 0.014 to 0.020 mm. Figure 19 is of a well extended young cercaria from a crushed snail, fixed with hot AFAG (alcohol-formalin-acetic acid-glycerin) fixing fluid added to a small amount of sea-water in a beaker in which the larvae were being whirled. Stained and mounted, it has a total length of 0.87 mm.; the body is 0.50 mm. long and 0.13 mm. wide at the collar; the acetabulum is 0.080 mm., the oral sucker is 0.057 mm., and the pharynx is 0.020 mm. in diameter. The tail is 0.037 mm. wide at the base. The body of the cercaria contains three types of glandular cells. There are three pairs of penetration glands situated in the preacetabular area, and four pairs of glands in the oral sucker, all of which open through pores at the anterior end of the body. The entire dorsal area of the body is occupied by cystogenous cells whose cytoplasm is filled with bacilliform granules. These granules do not stain with vital dyes. Other glandular cells, more ventral in location, stain faintly with eosin and erythrosin.

The reproductive organs are represented by two groups of deeply staining cells, one near the posterior end of the body and the other at the anterior margin of the acetabulum, and a strand of cells extending between the larger groups. The posterior group is the rudiment of the gonads and the anterior one of the copulatory organs. Only the major portion of the excretory system was observed. In immature larvae the tissues are fragile and disintegrate before the tubules are visible and in older ones the excretory ducts are obscured by the masses of glandular cells. Certain observations indicate that the flame cells are arranged in groups of three, but the complete pattern was not worked out. The system forms as separate left

and right components which meet and fuse at the posterior end of the body and the anterior portion of the tail. The two excretory pores are located on the sides of the tail, as shown in Figure 19. The vesicle is spherical to oval, thin-walled, and from either side a collecting duct passes forward, median to the digestive cecum, below the cecum at the level of the acetabulum, and then forward to the level of the oral sucker, where it recurves and passes posteriad. Near the middle of the body the recurrent duct divides into anterior and posterior branches. In the preacetabular area the collecting ducts have median and lateral branches and these branches subdivide in turn to form a ramified pattern as shown in Figure 20. In mature cercariae the collecting ducts contain spherical to oval concretions; in the postacetabular area the granules are larger, 0.005 to 0.01 mm. in diameter and more numerous, four or five at any level of the duct, whereas in the preacetabular ducts and their branches the granules are smaller, 0.003 to 0.005 mm. in diameter, and are arranged in single rows.

Himasthla mcintoshi n. sp.

This name is proposed for the seven specimens from the long-billed curlew, *Numenius americanus americanus*, collected by J. Bushman in Tooele County, Utah, on April 21, 1954 and deposited in the Helminthological Collection of the U. S. National Museum under the number 54.721. The species is named in honor of Dr. Allen McIntosh, Parasitologist in the Agricultural Research Service of the U. S. Department of Agriculture, in recognition of his contributions to helminthology and of the generous aid he has provided for other workers.

The worms are all sexually mature, with eggs in the uteri, chiefly in the initial one-half of the organ, with the terminal portion almost if not quite empty. Five of the worms are much bent or coiled and the one shown in Figure 16 is the only straight-bodied specimen. They vary from 6 to 11 mm. in length and from 0.5 to 0.7 mm. in greatest width. The anterior end bears a reniform collar which, in the two specimens in which they could be counted, is armed with 35 spines. There is a single row, interrupted ventrally, with 29 large spines, each 0.078 to 0.084 mm. in length and 0.02 mm. wide at the base, and at either end of the row, on the ventral side, there are three smaller corner-spines, about 0.055 mm. in length and 0.016 mm. wide at their bases. The lateral edges of the preacetabular region are curved ventrad and mediad, creating a median ventral depression (Fig. 17). When the body is contracted, the lateral walls are crenated and each annulus in the postacetabular region bears a circlet of small cuticular spines. In the preacetabular region the spines are closer together and arranged in an imbricated pattern, a cuticular arrangement characteristic of the genus *Himasthla*. The acetabulum is slightly less than twice its diameter from the anterior end of the body; it is directed antero-ventrad, protrudes slightly, and measures from 0.33 to 0.39 mm. in length and 0.31 to 0.35 mm. in width.

The mouth is subterminal, the oral sucker is 0.13 to 0.16 mm. in diameter, followed almost immediately by the pharynx, about 0.14 mm. long and 0.10 mm. wide. The esophagus extends almost to the acetabulum and the digestive ceca terminate blindly near the posterior end of the body.

The excretory pore is terminal, the vesicle is short and divides behind the posterior testis, with the collecting ducts passing forward just median to the

digestive ceca. They are clearly visible in the region between the anterior ends of the vitellaria and the acetabulum. Anterior to the acetabulum they are lateral in position and extend forward to the level of the oral sucker where they turn backward. Further details of the excretory system could not be observed.

The testes are oval, elongate, the posterior testis about its length from the posterior end of the body. There may be a short interval between the testes or they may be almost contiguous. The posterior testis is slightly larger than the anterior one and measures from 0.56 to 0.65 mm. in length and 0.22 to 0.28 mm. in width. Sperm ducts are not visible in the whole mounts; in most of the specimens the cirrus-sac extends about the diameter of the acetabulum behind that sucker; in the one shown in Figure 16, the cirrus-sac is coiled and consequently does not extend as far posteriad. The posterior one-half to two-thirds of the cirrus-sac is filled with a seminal vesicle and the anterior portion contains the eversible male duct, surrounded by secretory cells. The cirrus bears small recurved spines and the genital pore is median at the anterior margin of the acetabulum.

The ovary is spherical, 0.18 to 0.20 mm. in diameter, situated a short distance in front of the anterior testis. The oviduct arises at the posterior margin and the ootype and Mehlis' gland are posterior to the ovary. The vitellaria are lateral to and somewhat overlap the digestive ceca dorsally and ventrally. The follicles are spherical to oval, 0.04 to 0.065 mm. in diameter, continuous on both sides of the body, although somewhat reduced in one specimen at the level of the posterior testis. They extend from the posterior end of the body about two-thirds of the distance to the anterior end, terminating about two-thirds of the distance from the ovary to the acetabulum. Transverse ducts at the level of the ootype pass mediad to form a vitelline receptacle which discharges into the oviduct immediately before the ootype. The initial portion of the uterus is filled with spermatozoa. The eggs are broadly oval, those near the ovary average 0.100 by 0.076 mm., those farther along in the uterus are rounded, often collapsed, and may be slightly longer.

Himasthla mcintoshi agrees most closely with *H. rhigedana,* type of genus. Both are from species of *Numenius* and they are the only described species with more than 31 spines on the collar. Dietz reported a total of 34 to 38 spines in *H. rhigedana*, with 2, 3, or 4 corner-spines at each end of the row. In both of these species the corner-spines are very close together and often superimposed on those of the lineal row. Contractions of muscles in these locations produce variable orientation of the spines, so determination of their number and disposition is difficult. In Figure T of Dietz, the upper corner-spine on the left side could be interpreted either as a corner-spine or as the terminal spine in the collar-row. The two species differ in geographical distribution; *H. rhigedana* is from Arabia and *H. mcintoshi* from northwestern United States. Although the suckers do not differ greatly in size, *H. rhigedana* is more than twice as large as *H. mcintoshi,* the reproductive organs are much larger, although the eggs are smaller. The most obvious difference is in the disposition of the vitellaria; in *H. rhigedana* the vitellaria are interrupted at the testicular levels whereas in *H. mcintoshi* the follicles are continuous.

The type specimen is deposited in the U. S. National Museum Helminthological Collection under number 54,721.

Himasthla piscicola n. sp.

This species is based on specimens found by Dr. H. O. Ewert, veterinarian of the Zoological Society, Toledo, Ohio, in the alimentary canal of a fish, *Arapaima gigas,* from the Amazon River, Brazil. They were sent for determination to Dr. Leonard Allison of the Institute for Fisheries Research at the State Fish Hatchery, Grayling, Michigan. With the specimens there was the following information: "HISTORY; the 24 inch specimen arrived here in September. The fish ate in the first weeks, four to five goldfishes three inches long, daily, and came gradually down to one fish a day until he stopped eating around the 18th of December. In this week he vomited several small balls of mucus. Under the microscope, these balls appeared to consist of cells, mucus and many flagellates, *Octomitus intestinalis.* AUTOPSY; the abdominal investigation showed inflammation of the intestinal tract as well as the abdominal lining (peritonitis). The stomach lining was highly inflamed and congested. The stomach cavity was filled with a tenacious mucus and a certain parasite, which will be found separated on the accompanying slide." According to Allison (*in litt.*), the parasite was a trematode which had been mounted in water under a cover-glass and arrived perfectly dry. Other specimens were removed from the contents of the stomach which was preserved in water. Allison identified the worms as members of the genus *Himasthla.* Professor S. Yamaguti examined certain of the specimens and agreed with the generic determination, noting differences between these specimens and *H. tensa* Linton, 1940. Subsequently, Allison wrote Dr. G. R. La Rue, at the Animal Parasite Research Laboratory, Beltsville, Maryland, and sent him two of the worms in the belief that La Rue would write the description. But Dr. La Rue suggested that the writer examine the specimens and make the report. They are here described as a new species, *Himasthla piscicola.*

The two specimens measure 8.2 and 9.8 mm., respectively, in length. The larger one, shown in Figure 15, is designated as type. The organs of the smaller worm are almost as large as those of the type specimen. In the smaller one there are masses of spermatozoa in the initial portion of the uterus but no eggs. There are two eggs, one of them collapsed, in the uterus of the larger worm. In these specimens the reniform collar, open ventrally, delimits a short, flattened area at the anterior end of the body. The collar-spines are intact but other spines have been lost. There are 29 spines on the collar, 25 in the lineal row and two on either side behind the terminal ones. Those at the ventral corners are as large as those in the lineal row; they measure 0.085 mm. in length and 0.025 in maximum width. Behind the collar there is a short, neck-like constriction. The specimens are much extended, a result of their protracted immersion in water, and the uterine region between the cirrus-sac and the ovary is especially narrow. In the larger worm the width at the collar is 0.875 mm. The acetabulum is 0.44 mm. long and 0.50 mm. wide; it is about its diameter behind the collar. The oral sucker protrudes slightly and measures 0.18 by 0.19 mm. The pharynx is large, 0.24 mm. long and 0.11 mm. wide. The esophagus extends to the level of the acetabulum and the digestive ceca end blindly near the posterior end of the body. The testes are situated much nearer the middle than the posterior end of the body.

They partially overlap, the posterior third of the anterior testis is in the same zone as the anterior third of the posterior testis. They are elongate, slightly notched; the anterior one is 0.875 mm. long and 0.20 mm. wide, the posterior one is 0.89 mm. long and 0.20 mm. wide. The cirrus-sac extends posterior to the acetabulum more than twice the diameter of that sucker. A large seminal vesicle occupies the posterior half of the sac; the anterior portion of the vesicle and the succeeding duct are enclosed in a large, many-celled prostate gland. The cirrus is not protruded and no spines were observed. The ovary is situated near the middle of the body, only a short distance in front of the anterior testis, but would be relatively more posteriad if the uterus were filled with eggs. It measures 0.18 by 0.20 mm. The ootype complex is large, situated immediately posterior to the ovary; the initial portion of the uterus is filled with spermatozoa and there are two eggs in the uterus. One is collapsed, the other measures 0.114 by 0.064 mm. The vitelline follicles are continuous on each side of the body and extend from the posterior ends of the digestive ceca about three-fourths of the distance from the ovary to the posterior end of the cirrus-sac. The follicles would probably extend farther forward in more mature individuals.

Although the specimens are not mature, *H. piscicola* differs from all other adequately described species with 29 collar-spines in the position of the gonads, the shape and overlapping arrangement of the testes, and in the relative length of the posttesticular region of the body. *Himasthla piscicola* and *H. annulata* were found in the digestive tract of fishes from the Amazon River; it is possible that the two are identical, that some avian species is the natural host, and that the discovery of these worms in fish hosts is entirely incidental. The worms are similar in size, but the description and figures of Diesing give no information concerning internal morphology of *H. annulata* and it is quite impossible to determine whether the two are identical.

The type specimen of *H. piscicola* is deposited in the Helminthological Collection of the U. S. National Museum under the number 39,445.

Discussion

An investigation conducted by the U. S. Bureau of Commercial Fisheries is attempting to determine the causes for the decline in populations of *Mya arenaria* along the coast of New England and possible biological measures for control of the principal predators, the green crab (*Carcinus maenas*) and the horseshoe crab (*Limulus polyphemus*). *Mya arenaria* harbors the sporocysts and cercariae of *Cercaria myae* Uzmann, 1952; the larval stages of an as yet undetermined species of *Gymnophallus* (Stunkard and Uzmann, 1958). The palps and gills contain metacercariae of digenetic trematodes. Since the asexual generations of these metacercariae must occur in mollusks which live in the immediate vicinity of the infected clams, a survey of the more abundant species and those most likely to carry the trematode infections, is in progress. Furthermore, since the definitive hosts of these metacercariae are animals that feed on *M. arenaria*, examination of shorebirds has been started. To obtain precise information under controlled conditions, metacercariae from *M. arenaria* have been fed to laboratory-reared eider ducks,

herring gulls, common terns, white mice, and golden hamsters. The results, together with other pertinent information, are presented in this paper.

The metacercariae from *M. arenaria* proved to be larvae of three different species, all in the genus *Himasthla*, and the adults recovered from *L. argentatus* have been of value in resolving taxonomic problems in the genus. Typically, echinostomes are parasites of warm-blooded vertebrates and members of *Himasthla* have metacercarial stages in marine mollusks and mature in avian hosts. *Himasthla ambigua* Palombi, 1934 was described from metacercariae found in *Tapes decussatus* from the Gulf of Naples, but the adult stage is yet unknown. Palombi reported that the worms have 32 cephalic spines, that the infection is seasonal, and suggested that a bird, perhaps a migrant, is the final host. Elucidation of the life-cycle of *H. compacta* supports previous belief that species of *Himasthla* are parasites of birds and that the larvae occur in marine mollusks. Although adults of *H. compacta* are less than one-half the size of those of *H. quissetensis,* the cercariae of the two species are almost identical in size.

Since members of *Himasthla* typically are parasites of shore-birds, it is surprising that four species have been recorded from abnormal hosts, three from fishes and the fourth from a fruit-eating pigeon. Two species, *H. multilecithosa* from the pigeon and *H. piscicola* from *Arapaima gigas*, were taken from captive hosts and the time and place of infection are unknown. The finding of specimens of *Himasthla* in the digestive tract of marine and fresh-water fishes presents a biological anomaly. The fishes could have ingested a bird or its entrails that had fallen in the water and the proposed identity of *H. tensa* and *H. elongata* suggests such an explanation. *H. annulata* and *H. piscicola* were taken from the alimentary tract of fishes from the Amazon River of Brazil, and if the worms found in *A. gigas* were acquired in South America, they must have persisted for an unusually long time in the fish. The specimens were still juvenile, which indicates that they were recently ingested or that they fail to attain sexual maturity in the cold-blooded host. Since *H. annulata* (Diesing, 1850) and *H. piscicola* are from Amazonian fishes, it is possible that the two are identical, that some avian species is the natural host, and that the discovery of these worms in the digestive tract of fishes is entirely incidental.

Summary

The validity of species in the genus *Himasthla* is discussed; *Echinostoma annulatum* (Diesing, 1850) is transferred to *Himasthla* and *H. tensa* Linton, 1940 is suppressed as a synonym of *H. elongata* (Mehlis, 1831). A specimen from *Nycticorax nycticorax*, tentatively assigned to *H. elongata,* is very similar to *H. secunda* (Nicoll, 1906), which suggests the possibility that *H. secunda* may be a not-fully mature form of *H. elongata.* Three new species are described; *H. mcintoshi* from *Numenius americanus americanus* taken in Tooele County, Utah; *H. piscicola,* probably an accidental infection, from the South American fish, *Arapaima gigas;* and *H. compacta* from experimental infection of the herring gull, *Larus argentatus.* The life cycle of *H. compacta* has been traced; the asexual generations occur in *Hydrobia minuta*, the cercariae encyst in *Mya arenaria* and probably other mollusks.

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